

RAPTOR ABUNDANCE AND DISTRIBUTION IN THE LLANOS WETLANDS OF VENEZUELA

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ABSTRACT.—The Llanos of Venezuela is a 275 000-km² freshwater wetland long recognized as an important habitat for waterbirds. However, little information exists on the raptor community of the region. We conducted raptor surveys in the Southwestern and Western Llanos during 2000–02 and detected 28 species representing 19 genera. Overall, areas of the Llanos that we sampled contained 52% of all raptor species and more than 70% of the kites, buteos, and subbuteos known to inhabit Venezuela. Regional differences in the mean number per route for four of the 14 most common species, the Crested Caracara (*Caracara plancus*), Black-collared Hawk (*Busarellus nigricollis*), American Kestrel (*Falco sparverius*), and Osprey (*Pandion haliaetus*), were significant ($P < 0.0018$) in relation to the wet or dry seasons. Of the 14 less common species, six were detected in only one season (wet or dry). The Southwestern and Western regions of the Llanos support a rich raptor community composed primarily of nonmigratory wetland-dependent and upland-terrestrial species.

KEY WORDS: *Neotropics; Venezuela; Llanos; savanna; wetlands; roadside surveys.*

DISTRIBUCIÓN Y ABUNDANCIA DE RAPACES EN HUMEDALES DE LOS LLANOS DE VENEZUELA

RESUMEN.—Los llanos de Venezuela constituyen un humedal de agua dulce de 275 000 km² que ha sido tradicionalmente reconocido como un ambiente importante para las aves acuáticas. Sin embargo, existe poca información sobre la comunidad de rapaces de la región. Realizamos censos de aves rapaces en el sudoeste y el oeste de los llanos entre 2000 y 2002 y detectamos 28 especies que representaron 19 géneros. En total, las áreas de los llanos que censamos contuvieron el 52% de todas las especies de rapaces y más del 70% de los elanios, buteos y subbuteos que habitan en Venezuela. Las diferencias regionales en el número medio por ruta para cuatro de las 14 especies más comunes, *Caracara plancus*, *Busarellus nigricollis*, *Falco sparverius* y *Pandion haliaetus*, fueron significativas ($P < 0.0018$) con relación a las estaciones húmeda y seca. De las 14 especies menos comunes, seis fueron detectadas en una sola estación (húmeda o seca). Las regiones del sudoeste y del oeste de los llanos albergan una rica comunidad de aves rapaces compuesta primariamente por aves no migratorias que dependen de humedales y de especies terrestres de lugares elevados.

[Traducción del equipo editorial]

South America comprises 12% of the world's land surface, yet supports 28% of all raptors (Bierregaard 1998). Most South American raptors do not appear threatened globally, but more information is needed to confirm current assessments

and appropriately address threats (Bierregaard 1998, Bildstein et al. 1998). Community level raptor research in South America has been primarily focused in forest habitats (e.g., Thiollay 1984, Thiollay 1989, Alvarez et al. 1996, Manosa and Pedrocchi 1997, Manosa et al. 2003); thus, little is known about the raptor populations within the ex-

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tensive savanna and grassland regions of the continent. Raptor surveys in nine South American countries during 1979 detected the greatest number of species in the savannas, mixed riparian forests, pastures, and open areas of interior Venezuela (Ellis et al. 1990), indicating that these areas are important habitats for South American raptors. Furthermore, Neotropical raptors of open land and savanna habitats are currently threatened by habitat loss, including wetland depletion and landscape homogenization (Alvarez-Lopez and Kattan 1995).

In Venezuela, the savannas of the interior are part of an extensive (275 000 km²) wetland complex called the Llanos. The Llanos cover approximately 31% of Venezuela (Mittermeier et al. 2003) and are located in the latitudinal region characterized by the greatest avian endemism in the Northern Hemisphere (Bibby et al. 1992). Between 32–36 nonmigratory and North American migratory raptor species use some or all of the Llanos (Ferguson-Lees and Christie 2001, Hilty 2003). Although the natural history, biology, and habitat associations of some of these species have been studied locally (Mader 1981, 1982, Beissinger et al. 1988, Balgooyen 1989, Kirk and Currall 1994), community based, landscape-level surveys are lacking.

Our objective was to document and compare the species richness, relative abundance, and distribution of nonmigratory and migratory raptors in the savannas of the Southwestern and Western regions of the Venezuelan Llanos. We also compared these population parameters between the distinct wet and dry seasons that characterize the Llanos.

STUDY AREA

Venezuela supports 1381 species of birds (Hilty 2003) and is considered a globally important region of biodiversity in part due to its rich avifauna (Mittermeier and Mittermeier 1997, Myers et al. 2000). The Venezuelan Llanos is located between ca. 6–9°N and 63–71°W and is bordered by the Coastal Cordillera to the north, the Orinoco Delta and Guiana Shield to the east and southeast, Colombia to the south and southwest, and by the Andes Mountains to the northwest.

Annual rainfall in the Venezuelan Llanos ranges from 90–180 cm (Silva and Moreno 1993), with most rain falling and widespread flooding occurring from April through November (Cole 1986). In contrast, the late November–late April dry season typically is rain free (Troth 1979).

The Venezuelan Llanos is divided into three general areas: western, central, and eastern (Huber and Alcaron 1988). Covering 90 000 km², the western area comprises

35% of the freshwater wetland in Venezuela and spans north and west of the Orinoco River from ca. 69–71°W and 6–9°N (Bulla et al. 1990). This area is relatively flat, with elevation ranging from sea level at the Orinoco River to 155 m near the foothills of the Andes. The western area is further divided into two distinct regions known as the Southwestern and Western Llanos (Fig. 1; Huber and Alcaron 1988).

The Southwestern Llanos includes the vast open-savanna-wetland habitats that extend from the Meta and Orinoco rivers northwest to the agricultural-savanna-forest mosaic habitats of the Western Llanos. The Southwestern Llanos is characterized by poor soils, savanna habitats with small patches of trees, gallery forest, and extensive wet season flooding that renders the region largely unsuitable for agriculture (Huber and Alcaron 1988).

The Western Llanos encompasses the alluvial plains bordered by the foothills of the Andes and extends southeast to the open savannas of the Southwestern Llanos. This region is characterized by fertile soils and partial flooding that support agricultural production and native forests dominated by tree species similar to those of the Amazon basin (Huber and Alcaron 1988, Silva and Moreno 1993).

METHODS

Sampling Design. We surveyed raptors along the sparse network of roads accessible during both the wet and dry seasons in the Southwestern and Western Llanos (Fig. 1). Despite limitations inherent in roadside surveys (Millsap and LeFranc 1988, Bunn et al. 1995), such counts can be used to survey relative raptor abundance, community composition, and habitat associations across large landscapes (Woffinden and Murphy 1977, Thiollay 1978, Ellis et al. 1990, Sorley and Andersen 1994, Seavy and Apodaca 2002). However, roadside surveys in open habitats may be inadequate for detecting small and uncommon raptor species unless surveys incorporate frequent and regular stops (Whitacre and Turley 1990). Therefore, we used the North American Breeding Bird Survey model (Droege 1990) to establish stationary surveying points along road routes.

We placed 50 survey routes along roads where the overall distribution of survey routes was dictated by accessibility of roads during the wet season (Fig. 1). Each route was 22.5 km long with 16 sample points spaced 1.5 km apart (Jensen 2003: Appendix A). Each sample point was surveyed by a 2-person surveying team for 3 min to the right and left side of the road for a total of 6 min/point. All raptors were tallied within a 500-m radius as measured by rangefinder binoculars. Except for the King Vulture (*Sarcoramphus papa*), we did not tally Cathartid vultures. Scientific and common names of birds follow Ferguson-Lees and Christie (2001).

Raptors were surveyed during rainless periods of the day, primarily from 0700–1200 H, and never later than 1400 H. Surveys were conducted over ca. 6-wk periods twice each year between August 2000 and March 2002. The 6-wk periods coincided with the end of the wet (August–October) and dry seasons (January–March). We surveyed 27 routes in the wet season of 2000, 39 in the

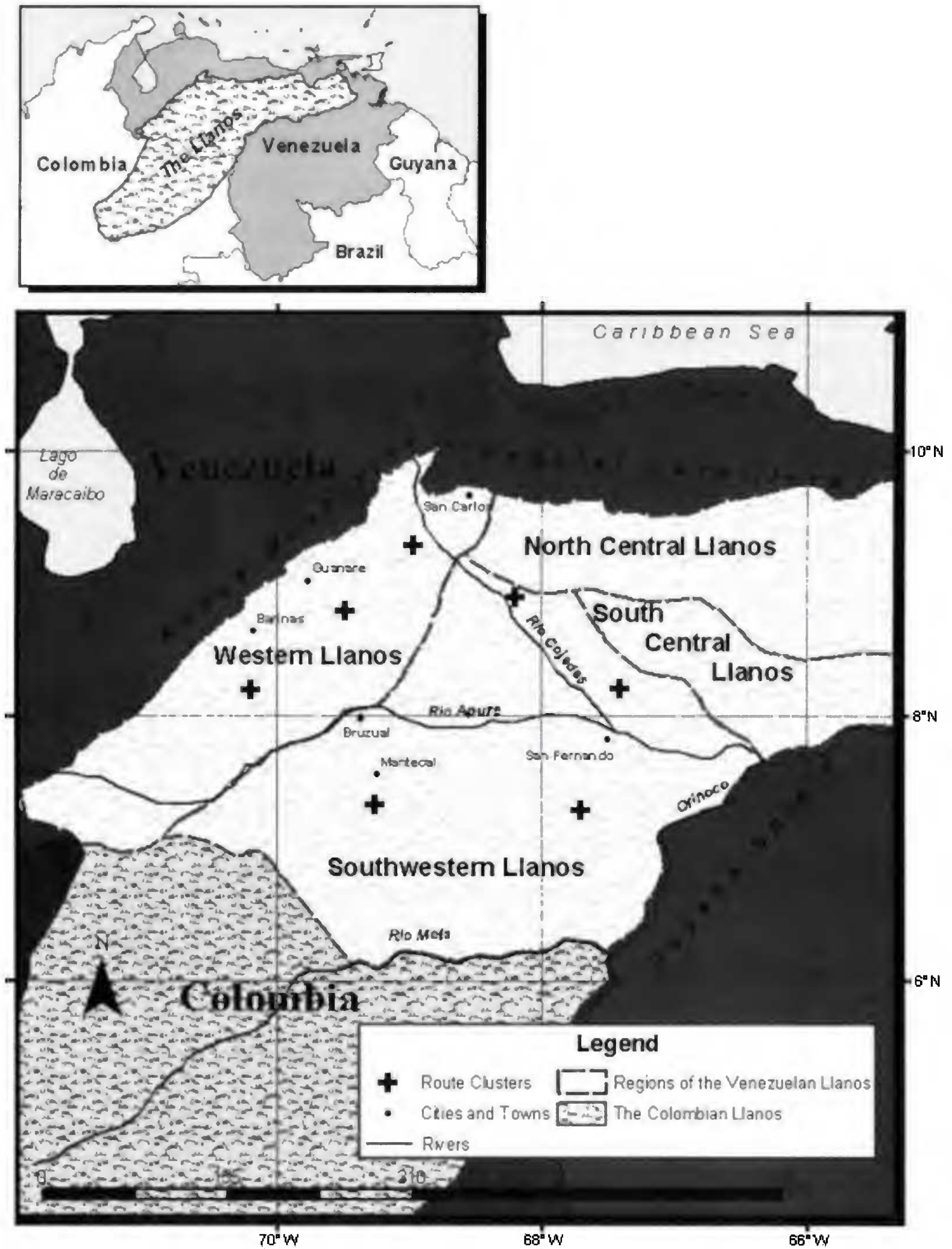


Figure 1. Study area map of the raptor survey during wet seasons 2000 and 2001 and dry seasons 2001 and 2002 in the Southwestern and Western Llanos of Venezuela. Route clusters are areas where groups of survey routes containing sample points are located.

dry season of 2001, 50 in the wet season of 2001, and 50 in the dry season of 2002.

Analysis. We calculated the total number of individuals detected on all surveys, as well as species totals, percent composition, and frequency of detection. We classified percent composition into four species abundance classes: Very common (10–26% of all individuals detected), Common (3–5%), Uncommon (1–2%), and Rare (<1%). We used EstimateS Version 6.0b1 software (Colwell 2000) to generate a species accumulation curve to evaluate the probability that our 2-yr 50-route roadside survey design was adequate for documenting all detectable raptor species.

We then calculated the mean number of individuals per species per route (mean number per route) by year, season, and region to investigate annual changes in abundance between the 2000 and 2001 wet seasons and the 2001 and 2002 dry seasons for each region. For this comparison we used the 27 routes surveyed during the first survey visit (wet season 2000) and resurveyed for the duration of the survey (2001 and 2002): Southwestern Llanos (15 routes) and Western Llanos (12 routes). Rare abundance class species were detected in numbers too low to meet the underlying assumptions for a *t*-test and were omitted from all subsequent statistical tests. For the 14 most common species, we used paired *t*-tests to evaluate four hypothesis (H_{01} : mean number per route Southwestern Llanos wet season 2000 = mean number per route Southwestern Llanos wet season 2001; H_{02} : mean number per route Southwestern Llanos dry season 2001 = mean number per route Southwestern Llanos dry season 2002; H_{03} : mean number per route Western Llanos wet season 2000 = mean number per route Western Llanos wet season 2001; H_{04} : mean number per route Western Llanos dry season 2001 = mean number per route Western Llanos dry season 2002). Differences were considered significant at $P < 0.10$ because we were interested in large-scale broad patterns. However, we used the Bonferroni Method to control for inflated experimentwise type I error rate resulting from simultaneous multiple comparisons (Beal and Khamis 1991). For all analysis, Bonferroni corrected significance for 56 comparisons was determined at ($P < 0.0018$).

We then combined data from both years to investigate seasonal and regional differences in species numbers, species diversity, community composition, and mean number per route for each species. During the 2-yr study, 50 routes were surveyed (Southwestern Llanos 28 routes, Western Llanos 22 routes). We surveyed 27 routes during both survey years (wet season 2000 and dry season 2001) and an additional 23 routes during the second survey year (wet season 2001 and dry season 2002). To standardize the number of individuals detected on the 27 routes surveyed over 2-yr, we averaged the number of individuals per survey point across survey years for each species. We then combined this 27-route average with the data from the 23 routes surveyed only during the second survey year to yield 50 total routes. Combining the data using this method preserved the majority of data collected, accounted for variation in numbers of individuals detected for each species on routes replicated over survey years, and preserved data from routes surveyed only during the second year.

We calculated species numbers and Simpson's Inverse Diversity Index ($D = 1/\sum pi^2$) for the wet and dry seasons within each region (Hayek and Buzas 1996). We also calculated Jaccard's Coefficient of Community Similarity to estimate the percent overlap between communities in both seasons and regions (Magurran 1988). Again, we used EstimateS version 6.0b1 software (Colwell 2000) to generate species accumulation curves for each regional and seasonal dataset to evaluate the probability that the number of routes surveyed in each region for each season were adequate for documenting all detectable raptor species.

To investigate seasonal and regional differences in numbers for each species, we first calculated the mean numbers per route for each region and season. To compare seasonal differences in mean numbers per route for the 14 most abundant species, we used paired *t*-tests to evaluate two hypothesis (H_{01} : mean number per route Southwestern Llanos wet seasons = mean number per route Southwestern Llanos dry seasons; H_{02} : mean number per route Western Llanos wet seasons = mean number per route Western Llanos dry seasons). For the same 14 species, we also used 2-sample *t*-tests to evaluate regional differences in mean numbers per route (H_{01} : mean number per route Southwestern Llanos wet seasons = mean number per route Western Llanos wet seasons; H_{02} : mean number per route Southwestern Llanos dry seasons = mean number per route Western Llanos dry seasons). The 14 rare abundance class species are presented only as present or absent for each region and season.

RESULTS

General Patterns. We counted 5735 raptors representing 28 species and 19 genera (Table 1). The four most abundant species, Crested Caracara (*Caracara plancus*), Yellow-headed Caracara (*Mitvago chimachima*), Savanna Hawk (*Buteogallus meridionalis*), and Roadside Hawk (*Buteo magnirostris*), comprised 72% of all individuals and were seen on 98–100% of all routes. Four additional species were classified as common and together comprised 15% of all individuals. These were the Black-collared Hawk (*Busarellus nigricollis*), White-tailed Hawk (*Buteo albicaudatus*), Snail Kite (*Rostrhamus sociabilis*), and American Kestrel (*Falco sparverius*). Six additional species were uncommon and represented 10% of all detections. They were the Aplomado Falcon (*Falco femoralis*), Great Black Hawk (*Buteogallus urubitinga*), White-tailed Kite (*Elanus leucurus*), Crane Hawk (*Geranospiza caerulescens*), Laughing Falcon (*Herpetotheres cachinnans*), and Osprey (*Pandion haliaetus*). Fourteen additional species comprised the remaining 3%. Species classified as common were detected on 52–84% of all routes, whereas uncommon species were detected on 44–78% routes. The 14 rare species were detected on

Table 1. Species detected during raptor surveys in the Southwestern and Western Llanos of Venezuela during wet seasons in 2000 and 2001 and dry seasons in 2001 and 2002. Species are listed in order of relative abundance based on percent composition. English common names and taxonomy follow Ferguson-Lees and Christie (2001).

| RELATIVE ABUNDANCE CLASS ^a | SPECIES | STATUS ^b | TOTAL NUMBER | PERCENT COMPOSITION | FREQUENCY OCCURRENCE (%) ^c |
|---------------------------------------|---|---------------------|--------------|---------------------|---------------------------------------|
| Very common | Crested Caracara (<i>Caracara plancus</i>) | R | 1473 | 26 | 100 |
| | Yellow-headed Caracara (<i>Mitvago chimachima</i>) | R | 1061 | 19 | 100 |
| | Savanna Hawk (<i>Buteogallus meridionalis</i>) | R | 1005 | 18 | 98 |
| Common | Roadside Hawk (<i>Buteo magnirostris</i>) | R | 604 | 11 | 98 |
| | Black-collared Hawk (<i>Busarellus nigricollis</i>) | R | 269 | 5 | 84 |
| | Snail Kite (<i>Rostrhamus sociabilis</i>) | R | 226 | 4 | 68 |
| | American Kestrel (<i>Falco sparverius</i>) | R/NAM | 183 | 3 | 52 |
| | White-tailed Hawk (<i>Buteo albicaudatus</i>) | R | 155 | 3 | 72 |
| | Aplomado Falcon (<i>Falco femoralis</i>) | R | 113 | 2 | 78 |
| | Great Black Hawk (<i>Buteogallus urubitinga</i>) | R | 110 | 2 | 58 |
| Uncommon | White-tailed Kite (<i>Elanus leucurus</i>) | R | 137 | 2 | 70 |
| | Crane Hawk (<i>Geranospiza caerulescens</i>) | R | 74 | 1 | 56 |
| | Laughing Falcon (<i>Herpetotheres cachinnans</i>) | R | 70 | 1 | 44 |
| | Osprey (<i>Pandion haliaetus</i>) | NAM | 66 | 1 | 48 |
| | King Vulture (<i>Sarcoramphus papa</i>) | R | 41 | 0.7 | 24 |
| Rare | Harris's Hawk (<i>Parabuteo unicinctus</i>) | R | 36 | 0.5 | 28 |
| | Grey-lined Hawk (<i>Buteo nitidus</i>) | R | 27 | 0.5 | 28 |
| | Zone-tailed Hawk (<i>Buteo albonotatus</i>) | R | 19 | 0.3 | 32 |
| | Slender-billed Kite (<i>Rostrhamus hamatus</i>) | R | 19 | 0.3 | 16 |
| | Bat Falcon (<i>Falco ruficularis</i>) | R | 16 | 0.3 | 24 |
| | Plumbeous Kite (<i>Ictinia plumbea</i>) | R | 9 | 0.2 | 14 |
| | Hook-billed Kite (<i>Chondrohierax uncinatus</i>) | R | 5 | 0.08 | 10 |
| | Long-winged Harrier (<i>Circus buffoni</i>) | R | 5 | 0.09 | 6 |
| | Common Black Hawk (<i>Buteogallus anthracinus</i>) | R | 5 | 0.09 | 10 |
| | Peregrine Falcon (<i>Falco peregrinus</i>) | NAM | 5 | 0.09 | 8 |
| | Short-tailed Hawk (<i>Buteo brachyurus</i>) | R | 5 | 0.09 | 6 |
| | Grey-headed Kite (<i>Leptodon cayanensis</i>) | R | 3 | 0.05 | 4 |
| | Pearl Kite (<i>Gampsonyx swainsonii</i>) | R | 3 | 0.05 | 6 |

^a Relative abundance class: Very common = 10–26% of all individuals detected; Common = 3–5%, Uncommon = 1–2%, Rare = <1%.

^b Status: R = nonmigratory population, NAM = North American migratory population, R/NAM = nonmigratory and North American migratory populations.

^c Frequency of occurrence: the percent of routes on which a species was detected.

≤32% of all routes. There were three species of North American migrants: Osprey, American Kestrel, and Peregrine Falcon (*Falco peregrinus*). The Osprey and Peregrine Falcon combined comprised 1.2% of all individuals seen. In contrast, the American Kestrel comprised 3%, having both nonmigratory and migratory populations (Hilty 2003). At least one of these three species was seen at least once on 82% of routes.

The species accumulation curve indicated the number of routes surveyed over the two survey years was adequate for documenting all species detectable by roadside point count surveys in the

study area (Fig. 2). Specifically, all 28 species were detected with 34 routes (68% of all routes surveyed).

Yearly Comparisons. Among the 14 most common species there were no regional or seasonal differences ($P > 0.0018$) in mean number per route between survey years (Table 2).

Regional and Seasonal Patterns. The greatest number of species, 25, was detected in the Southwestern Llanos during the wet season and in the Western Llanos during the dry season (Fig. 3). Although species numbers were equal between regions, diversity was higher in the Western Llanos

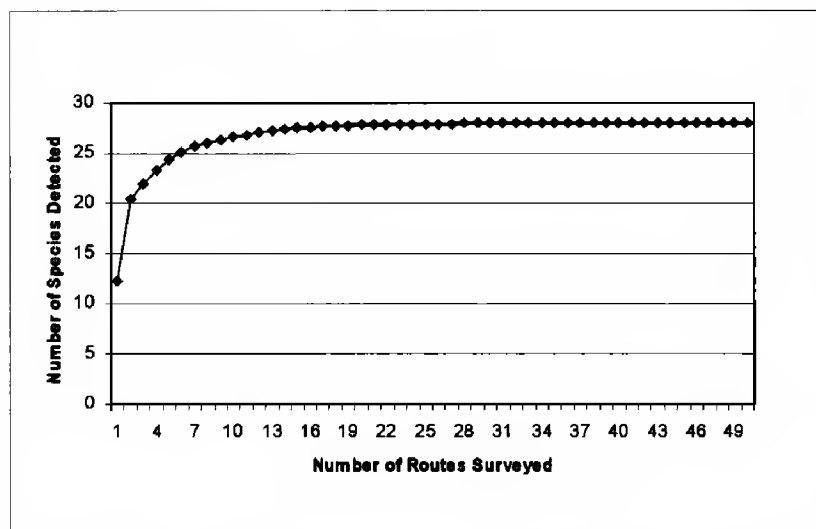


Figure 2. Species accumulation graph of raptor species detected on 50 survey routes in the Southwestern and Western Llanos of Venezuela during the wet seasons in 2000 and 2001 and dry seasons 2001 and 2002.

during both seasons. Species accumulation curves indicated the number of routes surveyed during each season was adequate to detect the majority of species for both regions (Fig. 4).

The raptor community (Jaccard's Coefficient of Community Similarity) in the Southwestern versus Western Llanos differed by 12%, both in the wet and dry seasons. For seasons combined, 25 species were detected in each region, of which 22 species were shared between regions. The seasonal changes in community composition within regions (26%) were greater than the regional differences within the wet and dry season (12%).

Four of the 14 most common species exhibited regional differences ($P < 0.0018$) in mean number per route in relation to the wet or dry seasons (Table 3). The Crested Caracara ($P < 0.001$) and Osprey ($P < 0.001$) were more numerous in the Southwestern Llanos than the Western Llanos during the wet season. The Black-collared Hawk ($P = 0.001$) was more numerous in the dry season in the Southwestern Llanos than the Western Llanos, whereas the American Kestrel ($P = 0.001$) was more numerous in the dry season in the Western Llanos than the Southwestern Llanos.

Of the 14 rare species, six were detected only during one season or region (Table 4). The Peregrine Falcon and Grey-headed Kite were seen only in the dry season, and the Pearl Kite and Slender-billed Kite were seen only in the wet season. The Common Black Hawk was detected only in the Southwestern Llanos in the wet season, and the Plumbeous Kite was detected only in the Western Llanos in the dry season.

DISCUSSION

General Findings. The savannas of the Southwestern and Western Llanos of Venezuela are particularly rich in raptors, supporting 52% (32 of 61) of all regularly occurring migrant and resident species found in Venezuela (Hilty 2003). Indeed, during our 2-yr study of the Venezuelan Llanos, these regions included 55% of all hawk species (10 of 18), 70% (7 of 10) of kite species, 67% (4 of 6) of vulture species, and 50% (3 of 6) of the regularly occurring North American migratory species (Hilty 2003). However, although the Llanos supported species assemblages equivalent to all other Venezuelan life zones for most raptors, we did not detect any of the eight eagle species that occur in Venezuela.

Except for the three common Cathartid species we did not count, we detected 24 of 27 resident species expected to occur in the Llanos (Hilty 2003). We did not detect three uncommon forest-dwelling raptors thought to occur in the region: the Collared Forest-Falcon (*Micrastur semitorquatus*), Bicolored Hawk (*Accipiter bicolor*), and Ornate Hawk Eagle (*Spizaetus ornatus*). We likely failed to see these species because of the inherent difficulty of detecting forest-dwelling species from roadside surveys (Millsap and LeFranc 1988).

Of the three North American migrant species we detected, two occur year-round in the Llanos. The American Kestrel occurs year-round in the Llanos because there are nonmigratory and migratory populations (Hilty 2003). Although the Osprey population is wholly migratory, the Osprey occurs year-round in the Llanos because first-year birds reaching the Llanos remain for at least 18 mo (Martell et al. 2001, Hilty 2003).

North American migratory species not seen during surveys were the Northern Harrier (*Circus cyaneus*), Broad-winged Hawk (*Buteo platypterus*), Swainson's Hawk (*B. swainsoni*), and Merlin (*Falco columbarius*). However, one Merlin was detected in the Llanos, but not on survey routes. Historical sightings of the Swainson's Hawk and Northern Harrier in the Llanos are considered accidental (Hilty 2003), and satellite-tracking of Swainson's Hawks confirms that their migrations to and from Argentina occur along the central and eastern slopes of the Andes (Fuller et al. 1998). The Broad-winged Hawk is thought to winter in portions of the Llanos west and north of our study area (Hilty 2003).

Table 2. Relative abundance class, species, and mean number of individuals (\pm SE) detected per route (mean/route) during raptor surveys in the Southwestern and Western Llanos of Venezuela during the wet seasons in 2000 and 2001 and the dry seasons in 2001 and 2002.

| RELATIVE ABUNDANCE CLASS ^a | SPECIES | SOUTHWESTERN LLANOS | | | | WESTERN LLANOS | | | |
|---|------------------------|---------------------|-------------------|------------------|------------------|------------------|-----------------|------------------|-----------------|
| | | WET ($N = 15$) | | DRY ($N = 26$) | | WET ($N = 15$) | | DRY ($N = 26$) | |
| | | 2000 | 2001 ^b | 2001 | 2002 | 2000 | 2001 | 2001 | 2002 |
| Very common | Crested Caracara | 11.27 \pm 2.88 | 11.53 \pm 2.38 | 12.26 \pm 2.60 | 14.04 \pm 1.78 | 1.75 \pm 0.63 | 2.83 \pm 0.49 | 5.31 \pm 1.24 | 5.00 \pm 1.00 |
| | Yellow-headed Caracara | 5.07 \pm 1.30 | 5.80 \pm 1.10 | 5.22 \pm 0.66 | 7.00 \pm 0.92 | 4.58 \pm 1.12 | 6.33 \pm 1.09 | 8.92 \pm 1.71 | 9.54 \pm 1.99 |
| Common | Savanna Hawk | 2.47 \pm 0.58 | 4.80 \pm 0.97 | 6.19 \pm 1.17 | 6.48 \pm 1.18 | 1.00 \pm 0.44 | 1.08 \pm 0.53 | 10.92 \pm 3.71 | 7.77 \pm 1.99 |
| | Roadside Hawk | 2.07 \pm 0.79 | 2.60 \pm 0.88 | 2.41 \pm 0.53 | 3.74 \pm 0.80 | 1.83 \pm 0.60 | 3.33 \pm 0.66 | 3.38 \pm 0.81 | 3.00 \pm 0.60 |
| | Black-collared Hawk | 1.13 \pm 0.41 | 2.33 \pm 0.55 | 2.07 \pm 0.53 | 2.93 \pm 0.58 | 0.17 \pm 0.11 | 0.42 \pm 0.23 | 0.46 \pm 0.22 | 0.39 \pm 0.18 |
| | Snail Kite | 4.40 \pm 2.63 | 3.73 \pm 1.27 | 0.96 \pm 0.29 | 0.89 \pm 0.37 | 0.17 \pm 0.17 | 1.50 \pm 0.68 | 0 | 0.31 \pm 0.13 |
| Uncommon | American Kestrel | 0 | 0.13 \pm 0.09 | 0.22 \pm 0.10 | 0.22 \pm 0.11 | 1.92 \pm 0.74 | 2.33 \pm 1.29 | 2.31 \pm 0.74 | 3.54 \pm 1.23 |
| | White-tailed Hawk | 1.40 \pm 0.38 | 1.73 \pm 0.47 | 0.07 \pm 0.27 | 1.00 \pm 0.26 | 0.25 \pm 0.18 | 0.33 \pm 0.33 | 1.08 \pm 0.45 | 0.92 \pm 0.37 |
| | Aplomado Falcon | 0.73 \pm 0.23 | 1.13 \pm 0.39 | 0.41 \pm 0.15 | 1.11 \pm 0.36 | 0.50 \pm 0.26 | 0.75 \pm 0.28 | 0.54 \pm 0.18 | 0.54 \pm 0.18 |
| | Great Black Hawk | 0 | 0.53 \pm 0.24 | 0.89 \pm 0.24 | 1.11 \pm 0.40 | 0 | 0.17 \pm 0.17 | 0.15 \pm 0.15 | 0.31 \pm 0.18 |
| | White-tailed Kite | 0.33 \pm 0.13 | 0.33 \pm 0.19 | 0.26 \pm 0.10 | 0.41 \pm 0.15 | 1.25 \pm 0.41 | 1.50 \pm 0.56 | 1.77 \pm 0.55 | 1.46 \pm 0.39 |
| | Crane Hawk | 0.33 \pm 0.21 | 0.27 \pm 0.18 | 0.30 \pm 0.12 | 0.78 \pm 0.18 | 0.08 \pm 0.08 | 0.08 \pm 0.08 | 0.23 \pm 0.17 | 0.23 \pm 0.12 |
| Laughing Falcon | Laughing Falcon | 0.07 \pm 0.07 | 0.27 \pm 0.19 | 0.04 \pm 0.04 | 0.19 \pm 0.13 | 0.42 \pm 0.26 | 0.33 \pm 0.26 | 0.54 \pm 0.27 | 0.39 \pm 0.21 |
| | Osprey | 0.87 \pm 0.39 | 0.73 \pm 0.23 | 0.30 \pm 0.12 | 0.48 \pm 0.22 | 0 | 0 | 0.15 \pm 0.15 | 0.39 \pm 0.18 |

^a Relative abundance class: Very common = 10–26% of all individuals detected; Common = 3–5%; Uncommon = 1–2%.

^b All comparisons were not significant ($P > 0.0018$).

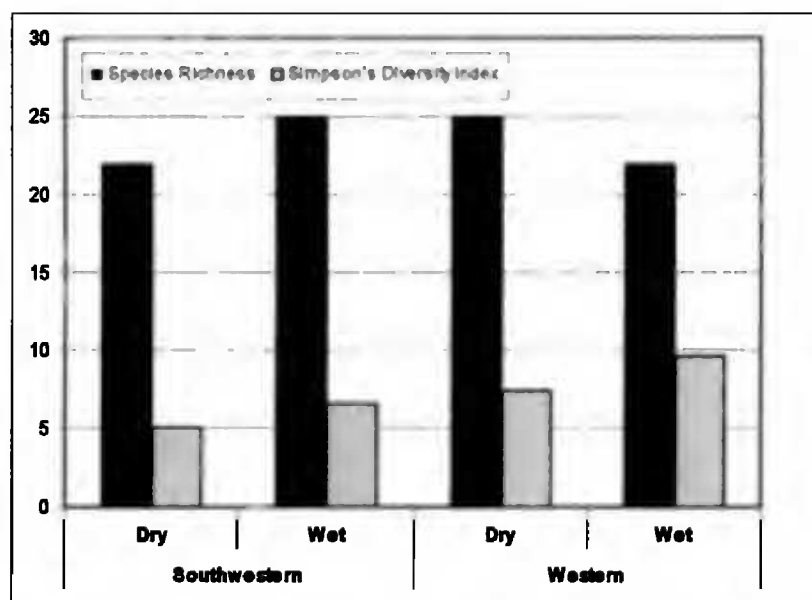


Figure 3. Raptor species numbers and diversity in the Southwestern and Western Llanos of Venezuela for combined years during the wet season (2000 and 2001) and the dry season (2001 and 2002).

Overall, the Southwestern and Western regions of the Llanos lacked the eagle diversity characteristic of African savannas (Thiollay 1978). Nonetheless, these Llanos regions supported numbers of raptor genera (21) similar to those found in the seasonally-flooded savannas and agricultural-forest

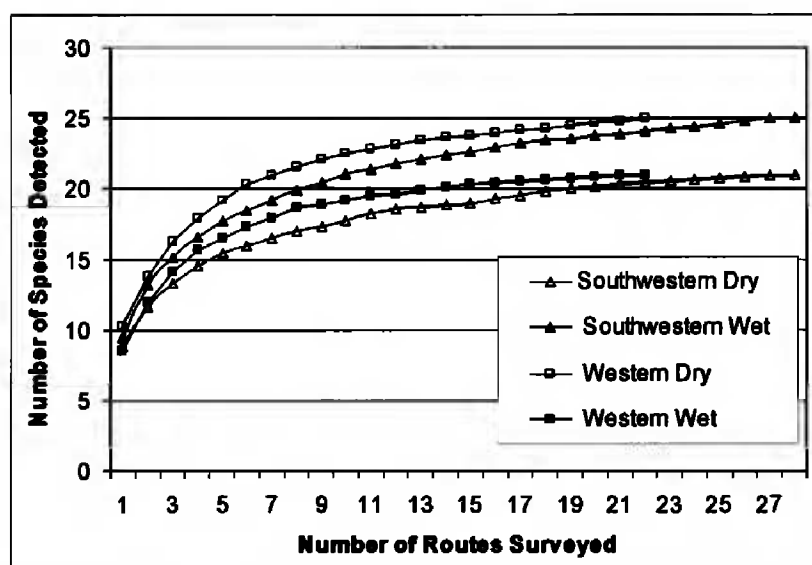


Figure 4. Species accumulation graphs for raptors detected in the Southwestern and Western Llanos of Venezuela for combined years during the wet seasons (2000 and 2001) and the dry seasons (2001 and 2002).

mosaic habitats of Kidepo Valley National Park of Uganda (22; Thiollay 1978). Consequently, migratory species in the Southwestern and Western Llanos only comprise a small portion of the raptor community (7%), whereas migratory species account for 33% of the raptor community in Kidepo Valley National Park of Uganda.

Table 3. Relative abundance of species and mean number of individuals (\pm SE) detected per route (mean/route) during raptor surveys for combined years in the wet (2000 and 2001) and the dry season (2001 and 2002) in the Southwestern and Western Llanos of Venezuela.

| RELATIVE ABUNDANCE CLASS ^a | SPECIES | STATUS ^b | SOUTHWESTERN (N = 28) | | WESTERN (N = 22) | |
|---------------------------------------|------------------------|---------------------|-------------------------------|------------------------------|------------------------------|------------------------------|
| | | | WET ^c | DRY ^c | WET ^c | DRY ^c |
| Very common | Crested Caracara | R | 10.21 \pm 1.37 ^d | 13.80 \pm 1.88 | 2.98 \pm 0.88 ^d | 6.00 \pm 1.62 |
| | Yellow-headed Caracara | R | 6.09 \pm 0.70 | 6.70 \pm 0.74 | 5.21 \pm 0.97 | 8.05 \pm 1.25 |
| | Savanna Hawk | R | 4.45 \pm 0.63 | 6.34 \pm 1.06 | 3.16 \pm 0.76 | 12.70 \pm 3.92 |
| | Roadside Hawk | R | 3.25 \pm 0.62 | 3.59 \pm 0.76 | 5.18 \pm 0.81 | 5.41 \pm 0.80 |
| Common | Black-collared Hawk | R | 2.36 \pm 0.53 | 2.73 \pm 0.55 ^D | 0.52 \pm 0.21 | 0.66 \pm 0.20 ^D |
| | Snail Kite | R | 3.00 \pm 0.94 | 0.93 \pm 0.35 | 0.73 \pm 0.22 | 0.23 \pm 0.09 |
| | American Kestrel | R/NAM | 0.25 \pm 0.13 | 0.23 \pm 0.10 ^D | 2.21 \pm 0.76 | 2.37 \pm 0.57 ^D |
| | White-tailed Hawk | R | 1.41 \pm 0.24 | 0.82 \pm 0.18 | 0.48 \pm 0.24 | 0.68 \pm 0.17 |
| Uncommon | Aplomado Falcon | R | 0.61 \pm 0.17 | 0.84 \pm 0.20 | 0.57 \pm 0.13 | 0.60 \pm 0.16 |
| | Great Black Hawk | R | 0.84 \pm 0.30 | 1.21 \pm 0.37 | 0.59 \pm 0.19 | 0.43 \pm 0.18 |
| | White-tailed Kite | R | 0.32 \pm 0.09 | 0.39 \pm 0.12 | 1.48 \pm 0.40 | 1.50 \pm 0.32 |
| | Crane Hawk | R | 0.30 \pm 0.10 | 0.61 \pm 0.14 | 0.27 \pm 0.11 | 0.55 \pm 0.19 |
| | Laughing Falcon | R | 0.23 \pm 0.12 | 0.18 \pm 0.13 | 0.93 \pm 0.27 | 1.09 \pm 0.38 |
| | Osprey | NAM | 0.93 \pm 0.21 ^d | 0.38 \pm 0.14 | 0 ^d | 0.28 \pm 0.11 |

^a Relative abundance class: Very common = 10–26% of all individuals detected; Common = 3–5%, Uncommon = 1–2%.

^b Status: R = resident species, NAM = North American migratory species, R/NAM = resident and North American migratory population.

^c Means denoted by "d" differed ($P < 0.0018$) between regions for the wet season. Means denoted by "D" differed ($P < 0.0018$) between regions for the dry season. All other comparisons were not significant ($P > 0.0018$).

Table 4. Rare species detected during raptor surveys for combined years in the wet (2000 and 2001) and the dry season (2001 and 2002) in the Southwestern and Western Llanos of Venezuela.

| RELATIVE ABUNDANCE CLASS ^a | SPECIES | STATUS ^b | SOUTHWESTERN (N = 28) | | WESTERN (N = 22) | |
|---|---------------------|---------------------|-----------------------|-----|------------------|-----|
| | | | WET | DRY | WET | DRY |
| Rare | King Vulture | R | X | | X | X |
| | Harris's Hawk | R | X | X | X | X |
| | Gray-lined Hawk | R | X | X | X | X |
| | Zone-tailed Hawk | R | X | X | X | X |
| | Slender-billed Kite | R | X | | X | |
| | Bat Falcon | R | X | X | X | X |
| | Plumbeous Kite | R | | | | X |
| | Hook-billed Kite | R | X | X | X | X |
| | Long-winged Harrier | R | X | X | | X |
| | Common Black Hawk | R | X | | | |
| | Peregrine Falcon | NAM | | X | | X |
| | Short-tailed Hawk | R | X | | X | X |
| | Grey-headed Kite | R | | X | | X |
| | Pearl Kite | R | X | | X | |

^a Relative abundance class: Rare = <1% of all individuals detected.

^b Status: R = nonmigratory populations, NAM = North American migratory population.

Regional and Seasonal Patterns. The Western Llanos was characterized by higher levels of raptor diversity. This region underwent a period of extensive deforestation prior to 1825, followed by forest regeneration through 1950, and another period of deforestation by 1975 (Veillon 1976). Forest exploitation cycles, coupled with agricultural activity and year-round water sources, have resulted in a dynamic mosaic of forest, savanna, agricultural, pasture, and early successional habitats that likely account for the high raptor diversity in this region.

Overall, raptor communities in the Southwestern and Western Llanos were similar. However, varying vegetation cover types, large-scale flooding, and the availability of year round water sources during the dry season almost certainly influence the raptor community. For example, Balgooyen (1989) reported the American Kestrel preferred the forest-agriculture mosaic habitats in the Llanos. Our data indicated this pattern was pronounced in the dry season, when American Kestrel numbers increased in the Western Llanos, likely due to the arrival of wintering North American migrants. Furthermore, several examples of seasonal influences are apparent in the Southwestern Llanos, where flooding of savanna and gallery forest is extensive in the wet season, but also where wetland complexes persist throughout the year. The higher numbers of the Black-collared Hawk in this region

during the dry season were likely explained by the presence of year-round wetland complexes. Similarly, the higher numbers of Osprey in the Southwestern Llanos versus Western Llanos during the wet season indicated that Osprey used both regions during the dry season, but first-year birds spent the wet season in the Southwestern Llanos, where flooding was extensive. Therefore, the year-round availability of wetland complexes and the extensive inundation of savanna in the wet season likely explains why these aquatic-dependent species are more abundant in this region.

Raptor Distribution. Our results on the relative abundance and distribution of the 14 most common species in our study were consistent with previous findings. However, 4 of 14 less common species were not expected to occur in the Llanos, or there was little information on their distribution and seasonal occurrence: Common Black Hawk (5 individuals), Pearl Kite (6), Plumbeous Kite (9), and Short-tailed Hawk (5). The Pearl Kite was reported as scarce or absent in the Llanos (Hilty 2003), but was detected in greater numbers than many species considered uncommon residents. Although the distribution of the Short-tailed Hawk was previously unknown in the Llanos (Hilty 2003), we detected this species in low numbers throughout the study area. Our observation that the Plumbeous Kite was absent during the wet season sug-

gests the Llanos population was similar to those of Central America, Mexico, and Trinidad. All of these raptors migrate southward in August and September and return north to breed in February and March (Ferguson-Lees and Christie 2001).

Conservation Implications. The rich raptor community of the Southwestern and Western Llanos is comprised of wetland-dependent and upland-terrestrial species, both nonmigratory and migratory, of which several appear seasonally nomadic and may depend on both regions as they move in and out in response to the wet and dry seasons. This pattern suggests that, at least in part, the diverse raptor community in the region owes its origins to a combination of a large landscape with a substantial seasonal influx of water and the forest-agricultural mosaic that creates a temporally and spatially diverse mix of habitats.

The Harris's Hawk (*Parabuteo unicinctus*), Savanna Hawk, and White-tailed Hawk are now absent from the Cauca Valley in Columbia as a result of landscape homogenization and wetland depletion (Alvarez-Lopez and Kattan 1995). We commonly detected the Savanna Hawk and White-tailed Hawk, and to a lesser extent the Harris's Hawk, throughout the Southwestern and Western Llanos, which suggests large-scale landscape homogenization and wetland degradation are not yet occurring in these regions. In contrast, because hawk-eagles may be less tolerant of human alterations on the landscape than many other raptors (Burnham et al. 1994), the Ornate Hawk-Eagle may have been affected by historical deforestation and subsequent lack of suitable habitats in these regions. However, with the exception of the Ornate Hawk-Eagle, the raptor community in the Llanos may represent a community model for Neotropical savanna-forest-agricultural regions.

Importantly, additional studies on the raptor community in the Llanos are required to better understand abundance patterns and seasonal fluctuations of raptors. Furthermore, research is needed to evaluate local areas where deforestation, intensive agriculture, and man-made impoundments are currently expanding, which may be useful for assessing the long-term stability of the current raptor community. Finally, comparisons between the Llanos and other Neotropical wetland-savanna complexes, such as the Brazilian Pantanal, will help determine the scope and representation of our findings.

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